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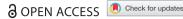
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Heritability of the elk hunting traits in the Finnish Jämthund population

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ABSTRACT

The aim of our study was to estimate the genetic parameters of elk hunting traits in the Finnish Jämthund population. The phenotype data included 40 402 trial observations recorded in Finland between 2012 and 2020 and the pedigree data included information of 34 495 Jämthunds. The genetic parameters of the elk hunting traits were estimated using a repeatability animal model. Season, place, and type of the trial, weather during the trial, and dog sex and age were considered fixed effects in the models, and trial judge and dog litter were treated as random effects. Variance components were estimated with the Al-REML method using the DMU-software. Heritability estimates were generally low (0.01-0.04). The highest estimated heritability was 0.04 for searching. Repeatability estimates for elk hunting traits varied between 0.04 and 0.14. Genetic correlations varied from very weak to very strong (-0.21-1.00) and were particularly strong between the barking traits.

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Heritability; elk hound; Jämthund; dog; hunting

Introduction

The Eurasian elk (Alces alces; hereafter elk) is the largest mammal living in Finnish forests. Unfortunately, elk can cause car collisions when crossing roads and can destroy small trees in recently planted forests by feeding on them during winter. Controlling the elk population by hunting is therefore important in Finland (Luke 2021). Elk hunting also provides recreational benefits, sports and competition, and is a source of meat.

Dogs are widely used for elk hunting in Finland. The Jämthund has been the most popular hunting breed in Finland for years, and it was also the second most popular breed in 2020, with 1 411 new registrations (KoiraNet, 2021). This large, Swedish elk hound breed was recognized as a separate breed from the Norwegian Elkhound Grey in 1946 (FCI 2019). The breed standard describes the Jämthund as strong, courageous, and energetic (FCI 2019).

To train, test, and compete against other dogs, thousands of official elk hunting trials are organized in Finland every year (SKL 2021a). Approximately 50% of all trial results relate to Jämthund dogs, and the remaining results relate to other elk hound breeds such as the Norwegian Elkhound Grey and Karelian Bear Dog (Koira-Net 2021; SKL 2021b). Participation in these trials is limited to certain breeds, and competing dogs should be registered and at least nine months old (SKL 2021a). Two field judges evaluate each dog's trial performance, and the results are verified by a chief judge (SKL 2021a). The trials are either long trials, where the dog attends a trial on any given day during the trial season from August to December, or regular one-day trials, where the trial areas and field judges are randomized. Each dog has a maximum of 360 min to search for elk and 300 min to work an elk, and each handler has an hour to recall a dog (or attempt to recall) their dog and put it on a lead after the dog has worked an elk (SKL 2021a).

Heritability estimates for the hunting traits have generally been low, ranging from 0.00 to 0.38, with considerable variation between different studies and hunting breeds (Karjalainen et al., 1996; Liinamo et al., 1997; Brenøe et al., 2002; Lindberg et al., 2004; Liinamo 2009; Arvelius & Klemetsdal 2013; Wetten & Aasmundstad 2014; Wetten et al., 2020). For example, Wetten and Aasmundstad (2014) estimated the heritability of searching as 0.05 in Norwegian Elkhounds, while the corresponding estimates in Finnish Spitz were 0.14 and 0.15 (Karjalainen et al., 1996). Likewise, heritability estimates for bark audibility have varied from 0.02 to 0.11 in Norwegian Elkhounds (Wetten & Aasmundstad 2014; Wetten et al., 2020). While heritability estimates for bark frequency have generally been the highest across breeds, estimates for obedience and cooperation between a dog and its handler have been low, usually ranging from 0.01 to 0.04, although some estimates have been as high as 0.21 (Karjalainen et al., 1996; Liinamo et al., 1997; Brenøe et al., 2002; Lindberg et al., 2004; Arvelius & Klemetsdal 2013; Wetten & Aasmundstad 2014; Wetten et al., 2020). Beyond genetic factors, the hunting traits are affected by sex, age, month, area, year, experience, and dog owner (Karjalainen et al., 1996; Liinamo et al., 1997; Lindberg et al., 2004; Liinamo 2009; Wetten & Aasmundstad 2014; Wetten et al., 2020).

Ranging rounds are an important part of hunting performance, as they affect the points awarded for searching and finding during the elk hunting trials. In practice, differences occur in the desired seeking width between hunting breeds. Elk hounds usually make long ranging rounds, up to ten kilometres in length, while bird dogs search over hundreds of metres (SKL 2021c). Ranging rounds may be either full, in which game is found, or blank, in which game is not found. Furthermore, the dog is expected to occasionally contact the handler, which shortens the ranging round distance. Optimum seeking width is therefore selected for instead of the longest distance. Heritability estimates for ranging rounds reported in previous studies have varied from 0.07 to 0.25 (Liinamo et al., 1997; Brenøe et al., 2002; Liinamo 2009; Arvelius & Klemetsdal 2013).

Using dogs with the highest genetic merit for breeding while maintaining a sufficient effective population size is important for improving hunting traits. Given the low heritability estimates for these traits, it is difficult to separate a dog with a high genetic merit from a well-trained dog based only on the dog's performance. Thus, it is important to consider all information from the relatives and to account for systematic effects when estimating breeding values and ranking the dogs. This may be achieved by the Best Linear Unbiased Estimation (BLUP) method. Our aim was to update the statistical models and the genetic parameters used in BLUP evaluation of hunting traits in Finnish Jämthunds. We additionally estimated the heritability of a range of new traits.

Material and methods

Data

The data set included 41 007 official Finnish elk hunting trial observations from 7 100 Jämthunds recorded between 2012 and 2020. The pedigree data included registry information of 34 495. After pruning the pedigree data included 8 757 animals that contributed to the variance component estimation (animals with observations and their ancestors up to four generations). Only dogs registered in the Finnish kennel Club (FKC) were included. The data contained 870 sires, and the

Table 1. Scoring in international elk hunting trial rules (SKL 2021a).

Section	Points × weight	Maximum points
Searching	0-10 × 1.5	15
Efficiency	$0-10 \times 1$	10
Bark to hold	$0-10 \times 1.5$	15
Bark quality	$0-10 \times 1.5$	15
Following	$0-10 \times 1$	10
Stopping	$0-10 \times 1$	10
Bark duration	$0-10 \times 0.5$	5
Bark audibility	$0-10 \times 0.5$	5
Bark frequency	$0-10 \times 0.5$	5
Obedience	$0-10 \times 1$	10
Total points		100

average number of offspring with records per-sire was eight. Both data sets were provided by Suomen Harmaa-hirvikoirajärjestö ry (SHHJ).

We analysed the following traits: searching, efficiency (in locating game), bark to hold (the game at bay), bark quality, following game, stopping game, bark duration, bark audibility, bark frequency and constancy (hereafter bark frequency), and obedience and cooperation (hereafter obedience) (Table 1). Obedience consists of three sub-sections: obedience during searching (0–2 points), obedience during working (0–5 points), and obedience after trial (0–3 points). The points awarded for obedience are the total points collected from the fore-mentioned sub-sections (0–10 points) (SKL 2021a). Only searching, obedience, and obedience during searching are evaluated if a dog does not find elk during the trial (SKL 2021a).

Ranging rounds distances (in kilometres) and time spent on the ranging rounds (duration, in minutes) were included in the analyses as median values for both full and blank rounds. Traits were divided into three categories: search and find traits (searching, efficiency, following, and ranging rounds), barking traits (bark to hold, bark quality, stopping, bark duration, and bark audibility and frequency), and obedience traits.

The final data included 404 chief judges. The number of observations excluded due to missing or inaccurate recordings was 110. We also discarded observations from any trials where a dog had been disqualified or barred, or where a judge or handler had chosen to interrupt the trial or withdraw the dog from the trial (a total of 286 observations). Observations from the ranging rounds that were three standard deviations from the mean were also set as outliers. The final data included 40 402 observations from 6 924 individuals. Descriptive statistics of the traits in the final data are given in Table 2.

Statistical analysis

The data set included 21 713 observations of males and 18 689 observations of females with an average of five

Table 2. Descriptive statistics of hunting traits.

Trait ^a	N	Min	Max	Median	Mean	SEM	SD	CV
Searching	40 402	0	10	8	7.36	0.01	1.45	0.20
Efficiency	30 314	0	10	9	8.56	0.01	1.60	0.19
Bark to hold	30 314	0	10	9	7.36	0.02	3.15	0.43
Bark quality	30 314	0	10	8	7.21	0.02	3.29	0.46
Following	30 314	0	10	10	9.07	0.01	1.79	0.20
Stopping	30 314	0	10	10	7.55	0.02	3.26	0.43
Bark duration	30 314	0	10	10	7.58	0.02	3.47	0.46
Bark audibility	30 314	0	10	10	8.24	0.02	2.97	0.36
Bark frequency	30 314	0	10	8	7.76	0.02	2.94	0.38
Obedience	40 402	0	10	4	4.16	0.01	2.35	0.56
Obedience during searching	40 402	0	2	2	1.82	0.00	0.41	0.23
Obedience during working	30 314	0	5	1	2.06	0.01	1.65	0.80
Obedience after trial	30 314	0	3	1	1.06	0.01	1.04	0.98
Distance full, km	29 513	0.1	12.70	1.80	2.62	0.01	2.37	0.91
Duration full, min	29 382	1	127.00	20.00	27.71	0.14	24.69	0.89
Distance blank, km	30 332	0.1	13.10	2.00	2.72	0.01	2.36	0.87
Duration blank, min	30 322	1	141.50	24.00	31.66	0.15	26.33	0.83

^aThe unit for the trait is points except for the ranging rounds.

observations per dog. Hence, a repeatability animal model was used. Fixed effects considered were overall mean, sex, trial type (regular or long trial), snow cover, finding an elk (in searching, obedience, and obedience during searching), and age at the time of trial. Approximately one third of the observations were from long trials.

If snow cover was less than 1 cm in depth, the trial was considered to be carried out on bare ground (ca. 65% of the trials). Elk were found in 75% of the trials. Dog age varied, and hence the dogs were divided into five groups based on their age at the time of trial: undertwo-year-olds were in group 1, two-year-olds in group 2, three-year-olds in group 3, four-year-olds in group 4, and older individuals in group 5. Groups 1, 2, 3, 4, and 5 had 13 481; 10 896; 6 500; 3 841; and 5 684 dogs, respectively. Furthermore, we created a season*kenneldistrict variable, which combined the year, month, and location of the trial based on kennel district (SKL 2022). Smallest kennel districts were combined based on locational similarity, and the number of observations in the kennel districts varied from 1 051 to 4 866. The annual number of trials varied from 3 896 to 5 196. December was the most popular trial month, with a total of 14 222 observations, whereas trials carried out in August were considered to have been performed in September due to their low number. The number of trials carried out in September, October, and November were 10 485; 7 239; and 8 456, respectively. Finally, dogs born on the same day from the same parents were considered to be from the same litter. The data included 2 300 litters.

The final models were composed using backward elimination in RStudio 1.1.136 (RStudio Team 2020). The significance of the fixed effects was tested using ANOVA. The judge and litter effects were considered random effects in the final models due to their large numbers.

Variance components and correlations were estimated using the AI-REML approach in the DMU-software package (version 6, release 5.2, Madsen & Jensen 2013). The linear model was y = Xb + Ki + LI + Wpe + Za + e, where y, b, j, l, pe, a, and e are the vectors of observations, fixed effects, judge effects, litter effects, permanent environmental effects, animal effects, and residuals respectively. X, K, L, W, and Z are the corresponding incidence matrices. The random effects were assumed to be normally distributed with expected values of 0 and var $(\mathbf{j}) = \mathbf{I}\sigma_{\mathbf{j}}^2$, $var(\mathbf{I}) = \mathbf{I}\sigma_{\mathbf{j}}^2$, $var(\mathbf{pe}) = \mathbf{I}\sigma_{\mathbf{pe}}^2$, $var(\mathbf{a}) = \mathbf{A}\sigma_{\mathbf{a}}^2$, and $var(\mathbf{a}) = \mathbf{A}\sigma_{\mathbf{a}}^2$ (e) = $I\sigma_{e}^2$, where I is a diagonal matrix and A is the additive relationship matrix between the animals. Corresponding variances of the judge, litter, permanent environment, and animal (additive genetic component) and residual effects are σ_i^2 , σ_l^2 , σ_{pe}^2 , σ_a^2 , and σ_e^2 , respectively. Heritability was calculated as $h^2 = \sigma_a^2/\sigma_P^2$, where σ_a^2 is the additive genetic variance and σ_p^2 is the phenotypic variance ($\sigma_p^2 = \sigma_i^2 + \sigma_l^2 + \sigma_{pe}^2 + \sigma_a^2 + \sigma_e^2$). Repeatability was calculated as $r = (\sigma_a^2 + \sigma_{pe}^2)/\sigma_p^2$.

Correlations between the traits were based on twotrait model with $\mathbf{A} \otimes \mathbf{G}$, $\mathbf{I} \otimes \mathbf{Pe}$, and $\mathbf{I} \otimes \mathbf{R}$, where \otimes is the Kronecker product and \mathbf{G} is a 2 \times 2 matrix of additive genetic variances of the traits in the diagonal and covariances between the traits in the off-diagonals, I is an identity matrix, and Pe and R are (co)variance matrices for permanent environmental and residual effects, respectively. Standard errors of the heritability and correlations estimates were based on Taylor series approximation.

Results

Systematic effects

Sex, snow, and trial type affected a dog's performance in most elk hunting trials (Attachment Tables S1 and S2). Sex had a significant effect on all traits other than the duration of the blank ranging rounds and total points received for obedience. In general, males performed

better than females. Only in obedience during searching did the females receive more points than the males. In addition, males covered larger ranging rounds, and consequently, spent more time in full ranging rounds.

Snow had a significant effect on the all traits. Snow cover improved performance in all traits other than following. Additionally, the rounds were shorter and, consequently, less time was spent ranging when there was snow. Trial type affected the performance of all traits, blank ranging rounds excluded, and a long trial generally improved performance. Only in following and obedience during searching did the dogs receive more points in the regular trials than in the long ones. Long trials were characterized with shorter full rounds and subsequently, less time was spent on full ranging rounds in long trials than in regular ones. Blank ranging rounds were not affected by the trial type. Age affected all the traits, excluding obedience after a trial. However, of the traits related to barking, only bark to hold was affected by dog's age. Generally, dog performance was in accordance with its age - the oldest dogs received more points and, additionally, made longer rounds than the younger ones spending more time ranging than their younger counterparts. Additionally, both the oldest and the youngest dogs received the highest points in obedience during searching.

Finally, locating an elk affected searching, obedience, and obedience during searching, as expected based on the trial rules. Locating an elk during a trial improved dog performance in searching and obedience, but worsened performance in obedience during searching.

Heritability and repeatability estimates

Most traits were skewed to the left with highest points being awarded often. Logarithmic transformation was tested on traits associated to ranging rounds that were skewed to the right but had no significant effect on the results. Overall, heritability estimates and their standard errors were low. The highest heritability estimate (0.04) was estimated for searching. The most repeatable traits were searching, and the distance and duration of the blank ranging rounds. Estimates of variance components, heritability, repeatability, and their standard errors are given in Table 3.

Heritability estimates for the search and find traits varied between 0.01 for efficiency and 0.04 for searching. While searching had the highest repeatability (0.14), the remaining estimates varied from 0.04 to 0.11. The heritability estimates for barking traits varied between 0.01 and 0.02, while the repeatability estimates were low, ranging from 0.05 to 0.08. Heritability estimates for obedience traits were all 0.01. Additionally, the repeatability estimates for obedience traits varied from 0.06 to 0.07.

Genetic and phenotypic correlations

The genetic correlations estimated in this study were generally moderate or strong, varying from -0.21 to 1.00 (Table 4, Table 5 and Table 6). The phenotypic correlations estimated varied from -0.05 to 0.96 and were mostly weaker than the corresponding genetic correlations. For example, the genetic correlation between following and bark quality was 0.75 (SE 0.12), while the corresponding phenotypic correlation was 0.18. Additionally, the genetic correlation between following and frequency was 0.20 (SE 0.16) and the phenotypic correlation between them was 0.12. Similarly, the genetic correlation between searching and frequency was -0.21 (SE 0.14), while the corresponding phenotypic correlation was 0.12. Finally, the estimate of the genetic correlation between searching and bark quality was -0.04 (SE 0.16), and the corresponding phenotypic correlation was 0.10, while the estimate of the genetic

Table 3. Estimates of variance components and the heritability of elk hunting traits.

Trait	$\sigma_{\rm e}^2$	σ_{pe}^{2}	σ_{i}^{2}	σ_l^2	σ_{a}^2	h² (se)	r (se)
Searching	1.72	0.21	0.02	0.01	0.09	0.04 (0.01)	0.14 (0.01)
Efficiency	2.27	0.15	0.03	0.00	0.03	0.01 (0.00)	0.07 (0.01)
Following	2.90	0.19	0.01	0.01	0.10	0.03 (0.01)	0.09 (0.01)
Distance full round	5.26	0.12	0.05	0.00	0.10	0.02 (0.00)	0.04 (0.01)
Duration full round	573.24	14.70	3.45	0.00	11.66	0.02 (0.00)	0.04 (0.01)
Distance blank round	4.76	0.40	0.01	0.04	0.14	0.03 (0.01)	0.10 (0.01)
Duration blank round	589.48	50.78	0.86	1.59	22.08	0.03 (0.01)	0.11 (0.01)
Bark to hold	8.79	0.38	0.03	0.04	0.09	0.01 (0.00)	0.05 (0.01)
Bark quality	9.66	0.54	0.03	0.05	0.16	0.02 (0.00)	0.07 (0.01)
Stopping	9.74	0.37	0.03	0.03	0.15	0.01 (0.00)	0.05 (0.01)
Bark duration	10.97	0.49	0.07	0.09	0.14	0.01 (0.00)	0.05 (0.01)
Audibility	8.03	0.28	0.02	0.02	0.10	0.01 (0.00)	0.05 (0.01)
Frequency	7.53	0.45	0.02	0.12	0.20	0.02 (0.01)	0.08 (0.01)
Obedience	2.14	0.14	0.02	0.01	0.02	0.01 (0.00)	0.07 (0.01)
Obedience during searching	0.15	0.01	0.00	0.00	0.00	0.01 (0.00)	0.06 (0.01)
Obedience during working	1.05	0.07	0.02	0.01	0.01	0.01 (0.00)	0.06 (0.01)
Obedience after trial	0.95	0.06	0.01	0.01	0.01	0.01 (0.00)	0.06 (0.01)

Table 4. Correlations between the search and find traits. Genetic correlations and their standard errors (in parentheses) in the upper diagonal and phenotypic correlations in the lower diagonal.

Trait	Searching	Efficiency	Following	Distance full	Distance blank
Searching		0.94 (0.05)	0.35 (0.12)	0.71 (0.09)	0.84 (0.06)
Efficiency	0.43		0.19 (0.17)	0.85 (0.11)	0.65 (0.13)
Following	0.08	0.13		0.56 (0.14)	0.37 (0.14)
Distance full	0.20	0.26	0.02		0.87 (0.10)
Distance blank	0.37	0.10	0.01	0.61	

Table 5. Correlations between the barking traits. Genetic correlations and their standard errors (in parentheses) in the upper diagonal and phenotypic correlations in the lower diagonal.

Trait	Bark to hold	Bark quality	Stopping	Bark duration	Audibility	Frequency
Bark to hold		0.87 (0.10)	0.79 (0.11) ^a	0.87 (0.11)	0.83 (0.05) ^a	0.72 (0.11) ^a
Bark quality	0.61		0.98 (0.02) ^a	1.00 (0.01) ^a	0.95 (0.03) ^a	0.58 (0.09) ^a
Stopping	0.43 ^a	0.88 ^a		0.97 (0.02) ^a	0.90 (0.05) ^a	0.49 (0.11) ^a
Bark duration	0.59	0.96 ^a	0.89 ^a		0.94 (0.03) ^a	0.50 (0.11) ^a
Audibility	0.58 ^a	0.85 ^a	0.76 ^a	0.87 ^a		0.50 (0.10) ^a
Frequency	0.56 ^a	0.79 ^a	0.69 ^a	0.80 ^a	0.89 ^a	

^aRandom effects of trial judge and dog litter were not included in the models due to nonconvergence.

correlation between bark quality and the distance of the blank ranging round was 0.04 (SE 0.18), and the corresponding phenotypic correlation was 0.01.

The genetic correlations between the search and find traits varied from 0.19-0.94. Strongest genetic correlations were found between searching and efficiency and the weakest between efficiency and following. Phenotypic correlations varied from 0.01 to 0.61 – the strongest ones being between distance of full and blank ranging rounds and the weakest between following and distance of blank ranging rounds. Genetic correlations between the barking traits were generally strongest of all, varying from 0.49 to 1.00. In fact, the strongest genetic correlations were found between bark quality and stopping, between stopping and bark duration, and between bark quality and bark duration (0.97-1.00). The phenotypic correlations between the barking traits were strong or very strong, although, the ones related to bark to hold were weaker (0.43–0.61) than the other phenotypic correlations. Finally, the genetic correlations between the obedience traits varied from moderate to very strong (0.59–0.97).

Table 6. Correlations between the obedience traits. Genetic correlations and their standard errors (in parentheses) in the upper diagonal and phenotypic correlations in the lower diagonal.

Trait	Obedience during searching	Obedience during working	Obedience after trial
Obedience during searching		0.59 (0.25)	0.61 (0.20)
Obedience during working	-0.03		0.97 (0.24)
Obedience after trial	-0.05	0.37	

Phenotypic correlations were negative albeit very weak between obedience during searching and both obedience during working and obedience a after trial, while the phenotypic correlation between obedience during working and obedience after a trial was positive but weak. The standard errors of the genetic correlations were low, expect for the correlation between efficiency and following and for the correlations between traits in various categories. However, the standard error for the genetic correlation between following and bark quality was low.

Discussion

We estimated the heritability and repeatability of various elk hunting traits. The studied traits were searching, efficiency (in locating elk), bark to hold (elk at bay), bark quality, following and stopping an elk, bark duration, bark audibility and frequency, obedience, and the sub-sections of obedience: obedience during searching and working, and obedience after a trial. The ranging rounds dogs make to locate elk were the new traits that we studied, and the rounds were either full (an elk was found) or blank (no elk was found). Both the distance and duration of the ranging rounds were studied. We additionally estimated a range of genetic and phenotypic correlations between the elk hunting traits.

Fixed and random effects

Sex had a significant effect on all traits other than the duration of the blank ranging rounds and obedience (the total points), and males generally performed better than females. Wetten et al. (2020) have reported

similar results in Norwegian Elkhound. The differences in performance between sexes are likely to arise from differences in courage, softness (desire to please the handler), and muscle strength. In fact, males made longer ranging rounds than females, and additionally spent more time on full ranging rounds than females did. Conversely, females performed better than males in obedience during searching, while, surprisingly, males performed better in obedience during working and obedience after a trial. Indeed, trial judges may be prejudiced towards males being less obedient than females when an elk is found and may hence reward obedient males with extra points during working. Moreover, males may receive more obedience training due to a belief that they are less obedient during elk work.

Dogs may perform better in certain terrains, and weather and snow may affect how easy it is to search and follow game. For example, thick snow cover is expected to slow down dogs. However, while snow significantly affected all the traits, it surprisingly generally improved performance. For example, efficiency was improved in snow. Snow may cause a trail to remain longer on the ground, making it easier for a dog to find the elk - hence the higher points awarded for efficiency on snow cover than on bare ground. Conversely, snow cover decreased the points awarded for following, suggesting that dogs move slower in snow than the elk do. Indeed, the ranging rounds were shorter and took less time in snow cover than on bare ground. Finally, snow cover increased the points awarded for all barking traits, probably because winter causes the defoliation of trees that suppress sounds. Additionally, elk may be more timid at the end of winter than in autumn and stay at bay for longer hence the longer bark duration in snowy conditions. Stopping better in snow than on bare ground supports this conclusion. Likewise, dogs were more obedient in trials carried out on snow cover than on bare ground. However, this is likely due to the dogs becoming used to elk hunting by the middle of the hunting season, when there is more snow, compared with the beginning of the hunting season. Hence, obedience appears to increase with snow cover. Subsequently, as snow cover is related to trial timing, the season*kenneldistrict variable likely takes the snow situation during the trial into account to some extent because month, year, and location together affect how much snow is expected at certain times. However, interaction of the two variables, i.e. snow and season*kenneldistrict was not tested in our study, which may cause some bias in the estimates. Furthermore, while the number and behaviour of the elk, weather conditions, terrain, and residential density (enabling undesired wandering to property sites) are

partly taken into account by the season*kenneldistrict and snow variables, there is likely local variation within the kennel districts that is not considered.

As the season for elk hunting with dogs ends in midwinter and spring is the time for dog breeding, dogs may enter their first, likely long trial at a very young age. Trial type affected all the elk hunting traits excluding the ones related to blank ranging rounds. Dog performance was generally better in long trials than in regular ones. Only following and obedience during searching were better in regular trials, and this is likely because dogs attending regular trials are usually more experienced. Additionally, full rounds were shorter and took less time in long trials. Long trials serve as familiar hunting terrain for both the dog and the handler, and hence may provide more elk finds and improve performance, with easier elk finds shortening the full rounds. Likewise, age had a significant effect on all traits related to searching and obedience, excluding obedience after a trial. In general, the older the dog, the more points it received. As Karjalainen et al. (1996) and Liinamo et al. (1997) pointed out, improvement of the results with age implies relation of performance with acquired experience, training, and learning. Additionally, bark to hold improved with age, as was expected, while the remaining barking traits were not influenced by age, implying that barking is fully developed by the age of two years.

Finally, dogs received more points in searching and obedience when an elk was found. Dogs may work more eagerly when elk are in the area, and more points are therefore gained. Conversely, not finding an elk increased the points awarded for obedience during searching, likely because the dogs are in lower drive and are more prone to please the handler when an elk is not nearby.

The trial judge and dog litter were included as random effects in the models. The variances of the judge and litter effects were low in relation to the rest of the variance components. However, it is likely that the judges adjust their evaluation with certain environmental effects, as the judging criteria are targeted at good trial conditions (SKL 2021a). Hence, the evaluation of elk hunting trial may lack objectivity, which might lead to low estimates of heritability. Additionally, litter effect accounts for differences between the management practices of breeders that the puppies are exposed to prior to weaning but may additionally account for maternal effects, as they were not included in the final models. Adding the owner effect as random effects may explain the variation in trainable traits but would decrease the number of observations. Instead, adding more variables considering weather, for example information concerning rain and wind,



may improve estimating the genetic parameters, as the residual variances related to the traits were high.

Estimated heritability and repeatability

In previous studies, the heritability estimates for hunting traits have ranged from 0.00 to 0.38 for various breeds (Karialainen et al., 1996; Liinamo et al., 1997; Brenøe et al., 2002; Lindberg et al., 2004; Liinamo 2009; Arvelius & Klemetsdal 2013; Wetten & Aasmundstad 2014; Wetten et al., 2020). The heritability estimates and their standard errors were low in our study. The highest heritability estimated in this study was 0.04 for searching and the lowest was 0.01 for obediencerelated traits. Similarly, most of the bark-related traits had a low heritability estimate (0.01).

Previously reported estimated heritablities of searching for game have varied from 0.03 to 0.25 (Karjalainen et al., 1996; Liinamo et al., 1997; Brenøe et al., 2002; Liinamo 2009; Arvelius & Klemetsdal 2013; Wetten & Aasmundstad 2014; Wetten et al., 2020). In particular, the heritability estimates for searching reported for elk hounds have varied from 0.05 to 0.08 (Liinamo 2009; Wetten & Aasmundstad 2014; Wetten et al., 2020). The heritability estimated for searching was 0.04 in our study, similar to those reported previously, suggesting that the two elk hound breeds, Norwegian Elkhound and Jämthund, share the same amount of additive genetic variance related to searching. On the contrary, the heritability estimate for efficiency gained in our study (0.01) was lower than what has previously been reported in Norwegian Elkhound (0.05) (Wetten & Aasmundstad 2014; Wetten et al., 2020). Similarly, in previous studies, heritability estimates for following have varied from 0.04 to 0.08 in the two elk hound breeds (Liinamo 2009; Wetten & Aasmundstad 2014; Wetten et al., 2020), while the corresponding estimate in our study was 0.03.

Ranging distance varies between the breeds and types of hunting dogs. In previous studies, the heritability of ranging distance has varied from 0.07 to 0.25 for a variety of hunting breeds but has often been estimated from subjective evaluations of ranging distances (Liinamo et al., 1997; Liinamo 2009; Arvelius & Klemetsdal 2013). In our study, heritability was estimated from the ranging round medians. Nevertheless, the heritability estimates were low: 0.02 for full rounds and 0.03 for blank rounds. In comparison, Liinamo (2009) reported a higher heritability estimate for ranging rounds (0.07) for the two elk hound breeds mentioned previously. However, the two breeds were analysed jointly, resulting in increased additive genetic variance. Finally, the heritability estimates for ranging round duration estimated in our study were 0.02 and 0.03 for full rounds and blank rounds, respectively. The estimates were in accordance with what Liinamo et al. (1997) reported for ranging round duration in Finnish Hounds (0.02).

Heritability estimates regarding barking traits have varied from 0.02-0.22 in various hunting breeds (Karjalainen et al., 1996; Liinamo et al., 1997; Liinamo 2009; Wetten & Aasmundstad 2014; Wetten et al., 2020). In particular, the heritability estimates for frequency have generally been high: from 0.12 to 0.22 (Karjalainen et al., 1996; Liinamo et al., 1997; Liinamo 2009; Wetten & Aasmundstad 2014; Wetten et al., 2020). Frequency can be measured fairly objectively as counts per minute or subjectively as a merit score (a combination of objective and subjective measures), which may affect the heritability estimates. For example, Liinamo (2009) estimated a heritability of 0.06 for frequency when measured as a merit score and 0.22 when measured as counts per minute. In our study, frequency was measured as a merit score and had a heritability estimate of 0.02, yet it was lower than reported by Liinamo (2009) in elk hounds when estimated from merit scores (0.06). Consequently, using a count score instead of a merit score could have gained a higher heritability estimate for frequency in our study.

Heritability estimates for audibility have varied from 0.02 to 0.11 in elk hunting breeds (Liinamo 2009; Wetten & Aasmundstad 2014; Wetten et al., 2020). The heritability of audibility estimated in our study (0.01) was similar to what Wetten et al. (2020) reported in Norwegian Elkhound (0.02), but much lower than what Wetten and Aasmundstad (2014) reported for Norwegian Elkhound (0.11). Similarly, in our study, heritability estimated for bark to hold and bark quality, 0.01 and 0.02, respectively, were lower than what has previously been reported for Norwegian Elkhound: 0.05-0.08 for bark to hold and 0.06 for bark quality (Wetten and Aasmundstad 2014; Wetten et al., 2020). The heritabilities estimated for stopping and bark duration in elk hounds have not been reported previously. In our study, the estimated heritabilities for stopping and bark duration were 0.01 and 0.01, respectively.

Finally, heritability estimates for obedience (and cooperation) have generally been low (0.01–0.12), although estimates as high as 0.21 have been reported (Liinamo et al., 1997; Brenøe et al., 2002; Lindberg et al., 2004; Arvelius & Klemetsdal 2013; Wetten & Aasmundstad 2014; Wetten et al., 2020). In particular, heritability estimates for obedience (and cooperation) in Norwegian Elk hound have varied from 0.01 to 0.04 (Wetten & Aasmundstad 2014; Wetten et al., 2020). In our study, the heritability estimates for obediencerelated traits were 0.01. Environmental factors, for example training, clearly play a major role in obedience

and were not considered in our study. However, the kennel district likely accounts for training to an extent.

Besides the heritability estimates, repeatability estimates for hunting traits have also varied considerably in previous studies, ranging from 0.03 to 0.38 (Karialainen et al., 1996; Liinamo et al., 1997; Brenøe et al., 2002; Liinamo 2009; Arvelius & Klemetsdal 2013). Repeatability estimates found in our study were relatively low (0.04–0.15). The highest repeatability estimate was 0.14 for searching and the lowest was 0.04 for traits related to full ranging rounds. Repeatability estimates found by our study for following and efficiency, 0.09 and 0.07, respectively, were similar to those previously reported for Finnish Spitzes and Finnish Hounds (0.14-0.18 and 0.06, respectively) (Karjalainen et al., 1996; Liinamo et al., 1997).

Repeatability estimates for ranging rounds were significantly lower in our study than in previous studies, where they have varied from 0.19 to 0.38 (Liinamo et al., 1997; Brenøe et al. 2002; Arvelius & Klemetsdal 2013). The distance and duration of a full ranging round depends on where game is found, and hence, they are not expected to be as repeatable traits as are distance and duration of blank ranging rounds. Rather, the length of blank ranging rounds reflects how long a ranging distance the dog is willing to cover until possibly trying to contact the handler, while full ranging rounds reflect a dog's efficiency in locating game. Indeed, the repeatability estimates for blank ranging rounds found in this study (0.10-0.11) were approximately three times higher than those for full ranging rounds (0.04), which supports our conclusion. The repeatability estimate for the duration of full ranging rounds in our study was similar to what Liinamo et al. (1997) have reported in Finnish Hounds (0.03). A higher repeatability of ranging distances in our study could have been achieved by analysing each ranging round as an independent observation instead of using median values.

While frequency and audibility have generally had high repeatability (0.25-0.37) (Karjalainen et al., 1996; Liinamo et al., 1997; Liinamo 2009), the repeatabilities estimated for frequency and audibility in our study were 0.08 and 0.05, respectively. Our estimate was similar to what Liinamo (2009) estimated for frequency as a merit score (0.12) in the joint analysis of Norwegian Elkhounds and Jämthunds. Conversely, the heritability estimate for audibility in our study was much lower than what Liinamo et al. (1997) estimated for Finnish Hounds (0.25). It is possible that dogs adjust their barking based on elk behaviour, which may cause variation in both frequency and audibility, and result in low repeatability of the traits.

Finally, the repeatability estimates for obedience traits were low (0.06-0.07) in our study, while estimates in previous studies have varied from 0.11 to 0.22 (Liinamo et al., 1997; Brenøe et al., 2002; Arvelius and Klemetsdal 2013). As the distribution of points awarded in trials is skewed, a breed-specific evaluation could be used to reveal differences between the dogs.

Genetic and phenotypic correlations

Strong positive genetic correlations imply to evaluated traits that share the same genetic background. Many hunting traits are genetically correlated, but the correlations vary by traits. As an example, the genetic correlation between searching for and following game has varied between 0.31 and 0.79, while the genetic correlation between searching and barking traits generally varied from 0.14 to 0.29 (Karjalainen et al., 1996; Liinamo et al., 1997; Wetten et al., 2020). Furthermore, estimates of genetic correlations vary by breeds; while Liinamo et al. (1997) reported a genetic correlation of 0.07 between following and barking in Finnish Hounds, Wetten et al. (2020) reported corresponding correlations between 0.17 and 0.70 in Norwegian Elkhounds.

In our study, the genetic correlations of elk hunting traits varied from -0.21 to 1.00, while the phenotypic correlations varied from -0.05 to 0.96. Phenotypic correlations were generally weaker than the corresponding genetic correlations. However, within barking traits, many of the phenotypic correlations related to frequency were much stronger than the corresponding genetic correlations. This is likely because the genetic correlations related to frequency were weaker than the remaining correlations related to barking traits, which could, on the other hand, be caused by frequency being measured more objectively than the remaining bark-related traits. Moreover, the genetic and phenotypic correlations within barking traits were generally the strongest of all correlations estimated in this study and were additionally stronger than the estimates reported in previous studies. For example, in our study, estimates of genetic correlation between audibility and both bark to hold and bark quality, were 0.83 and 0.95, respectively, while Wetten et al. (2020) reported corresponding correlations of 0.21 and 0.30, respectively. Likewise, the estimated genetic correlation between bark to hold and bark quality was 0.87 in our study, while Wetten et al. (2020) reported a corresponding correlation of 0.56. On the other hand, the genetic correlation of 0.92 between audibility and barking estimated by Wetten et al. (2020) was higher than the genetic correlation estimated between audibility and frequency in our study

(0.50). Additionally, a very strong genetic correlation between searching and efficiency (0.94) found in this study was similar to what Wetten et al. (2020) have previously reported in Norwegian Elkhounds (0.97). In contrast, the estimate between searching and following reported in our study (0.35), was lower than those reported in previous studies (0.60-0.83) (Karjalainen et al., 1996; Liinamo et al., 1997; Wetten et al. 2020).

In general, the genetic correlations between various traits have been weak or moderate (Karjalainen et al., 1996; Liinamo et al., 1997; Wetten et al. 2020). For example, Karjalainen et al. (1996) reported an estimate of 0.31 as the genetic correlation between searching and frequency. On the contrary, the corresponding estimate in our study was -0.21. Similarly, genetic correlations of 0.49, 0.29, and 0.14 between searching and barking were estimated by Karjalainen et al. (1996), Liinamo et al. (1997), and Wetten et al. (2020), respectively, while for example, the genetic correlation between searching and bark quality was -0.04 in our study. Contrastingly, Liinamo et al. (1997) and Karjalainen et al. (1996) estimated genetic correlations of 0.07 and 0.55 between following and barking, respectively, and Wetten et al. (2020) reported estimates of genetic correlation between following and bark-related traits ranging from 0.17-0.70. In comparison, the genetic correlation between following and bark quality was 0.75 in our study, while the genetic correlation between following and frequency was 0.20 in our study.

Conclusions

Dog's sex and age, trial season, location, and type, and the weather during a trial affect dog performance in elk hunting trials. Long trials, snow, and dog maturity tend to improve hunting performance, and males generally perform better than females. Additionally, other barking traits than bark to hold are fully developed until the age of two years. While trial judge and dog litter have relatively marginal effects on elk hunting performance, many unknown systematic effects affect dog performance during trials, and the heritability estimates for the elk hunting traits are relatively low. Heritability estimates for the elk hunting traits found in this study varied between 0.01 and 0.04; the highest estimated heritability was 0.04 for searching. Likewise, the repeatability estimates calculated in this study were low. The highest estimated repeatability was 0.14 for searching, while the rest of the estimates varied from 0.04 to 0.11. Finally, we observed strong, positive genetic correlations between searching and efficiency, between obedience during working and obedience after the trial, and between the barking traits.

In conclusion, heritability and repeatability estimates for elk hunting traits are low, and many of the traits share a common genetic background.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

Data availability

The data supporting the findings of this study are available from Suomen Harmaahirvikoirajärjestö ry (SHHJ), Kylmälänkylä, Finland. Restrictions apply to the availability of these data, which were used under license for this study. Data are available from the corresponding author upon reasonable request and with permission from SHHJ.

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